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Image-based analyses from an online repository provide rich information on long-term changes in morphology and human perceptions of rhinos

Oscar E. Wilson[1] [iD] | Michael D. Pashkevich[2] [iD] | Kees Rookmaaker[3] [iD] |
Edgar C. Turner[2] [iD]

[1]Department of Geosciences and Geography, University of Helsinki, Helsinki, Finland

[2]Department of Zoology, University of Cambridge, Cambridge, UK

[3]Rhino Resource Center, Utrecht, The Netherlands

Correspondence
Oscar E. Wilson, Department of Geosciences and Geography, Physicum, Gustaf Hällströmin katu 2, 00560, Helsinki, Finland.
Email: oscar.wilson@helsinki.fi

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Abstract

1. Online image repositories can offer a freely accessible, information-rich and cost-effective alternative to museum collections for studying long-term changes in human interactions with nature and ecological and evolutionary change. The Rhino Resource Center (RRC) is one example, curated by experts and holding a collection of >4000 rhino images, including both artistic portrayals (1481–2021) and photographs (taken between 1862–2021), and representing a potentially valuable case study to investigate the utility of online image repositories for research into large vertebrates and, potentially, other well-recorded smaller taxa. The five extant species of rhino are all threatened by habitat loss and human hunting and therefore are an important focus for conservation research.

2. We used the RRC for two separate research approaches: (i) assessing the changing representations and human interactions with rhinos using 3158 images (1531 pieces of artwork and 1627 photographs); and (ii) determining to what extent morphological data can be extracted from photographs to assess changes in horn length over time, using a sample size of 80 photographs of rhinos taken in profile view.

3. We found that African rhino species have become more commonly depicted in images, compared to Asian rhino species over time. During the age of European imperialism (between the 16th and 20th centuries), rhinos were commonly portrayed as hunting trophies, but since the mid-20th century, they have been increasingly portrayed in a conservation context, reflecting a change in emphasis from a more to less consumptive relationship between humans and rhinos. Finally, we found evidence for declining horn length over time across species, perhaps related to selective pressure of hunting, and indicating a utility for image-based approaches in understanding societal perceptions of large vertebrates and trait evolution.

1 | INTRODUCTION

Museum collections represent a valuable and widely used data source in the study of evolutionary biology, ecology, conservation science and changing human interactions with nature, especially when associated with written records. By providing information on a diverse range of species, physical collections can act as a baseline against which to measure change (Pyke & Ehrlich, 2010; Suarez & Tsutsui, 2004; Waits et al., 1998). However, museum specimens are not the only long-term, large-scale datasets that are readily available to researchers. Humans have been producing images of nature for over 40,000 years (Aubert et al., 2018), and these images can be used to reconstruct both our changing relationships with species and changes in the natural world itself (Helgen et al., 2012; Kays et al., 2020; Morcote-Ríos et al., 2021; Packer & Clottes, 2000; Soubrier et al., 2016). For example, shifts away from consumptive uses of wildlife (e.g. hunting) towards less consumptive uses (e.g. wildlife tourism) have been identified in some groups (e.g. Macmillan & Phillip, 2008), through analyses of patterns in long-term image datasets. Increasingly, museum specimens themselves have also been digitised and images of them made available online (Hedrick et al., 2020), adding still further to this readily-available resource.

Large vertebrates, and especially mammals, are often considered the most charismatic and popular taxa (Luque & Courchamp, 2018), and are therefore particularly well represented in imagery. Rhinos are culturally significant in several parts of the world, are highly ranked among the world's most charismatic animal species (Luque & Courchamp, 2018) and feature heavily in historical and contemporary images and art, resulting in a particularly rich data-source for image-based research. For example, as early as 1515, an Indian rhino drowned off the coast of Italy during transport from Lisbon, Portugal, to the Vatican, and inspired a woodcut by Albrecht Dürer, which spread throughout Europe following the invention of printing (Quammen, 2000). Later, travelling menageries brought more rhinos to the public eye, conjuring fascination with these animals, and contributing to a vast record of historical images. One Indian rhino named Clara was toured across Europe between 1741 and 1756, inspiring a large volume of artwork (Rookmaaker, 1973). Such a wealth of long-term information provides a valuable opportunity to investigate the changing relationship and interactions between humans and rhinos, potentially informing action to increase public awareness and inform and promote conservation engagement.

Worldwide, there are five recognised extant rhino species (Groves & Grubb, 2011), across four genera (Family Rhinocerotidae; Order Perissodactyla; Liu et al., 2021). These are the white rhino *Ceratotherium simum*, black rhino *Diceros bicornis*, Indian rhino *Rhinoceros unicornis*, Javan rhino *Rhinoceros sondaicus* and Sumatran rhino *Dicerorhinus sumatrensis*. Three of the five species (the black

rhino, Javan rhino and Sumatran rhino) lie within the top twelve Evolutionarily Distinct and Globally Endangered (EDGE) species (Isaac et al., 2007), demonstrating their evolutionary distinctiveness, and all face conservation challenges as a result of human hunting for their horns, as well as habitat loss. The white rhino (Near Threatened) is the only species not currently threatened according to the IUCN Red List, with the Indian rhino listed as Vulnerable, and the black, Javan and Sumatran rhinos all listed as Critically Endangered. Modern poaching of rhinos is driven by high demands for horns, particularly in China and Vietnam, where the horn is used in traditional medicines, as a medium for carvings and as a financial investment in a valuable material (Cheung et al., 2018; Di Minin et al., 2015; Gao et al., 2016; Shepherd et al., 2018). This has resulted in rhino populations suffering precipitous declines. For example, one estimate suggests that 12,750 black rhinos were killed to provide the 36 tonnes of horn sold in Yemen between 1970 and 1986 alone (Leader-Williams, 1992). In Kenya, there were an estimated 20,000 black rhinos in 1991, but only 631 in 2014 (Thuo et al., 2015). Hunting, combined with habitat loss, has already led to the extirpation of the Sumatran rhino in mainland Southeast Asia (Lander & Brunson, 2018), and the species was declared extinct in Malaysia in 2019 (Gokkon, 2019). Similarly, the northern white rhino, a subspecies of the white rhino, is now considered functionally extinct, with only two surviving females remaining (Callender, 2021; Korody et al., 2021; Ryder et al., 2020).

Both modern poaching and historical trophy hunting are selective in the individuals killed. Given the high price of rhino horn, and increased social status for hunters that kill rhinos with the largest horns, we expect that individual rhinos with the longest horns might be targeted, consistent with similar selective hunting that has been reported in other taxa (Chiyo et al., 2015; Coltman et al., 2003; Festa-Bianchet et al., 2014). In other megaherbivores, selective harvesting of this kind has led to directional selection, whereby a strong selective hunting pressure has resulted in a reduction in the frequency of the desired trait (Coltman et al., 2003). For example, directional selection due to trophy hunting has driven declines in tusk size in elephants and horn length in wild sheep (Chiyo et al., 2015; Coltman et al., 2003; Festa-Bianchet et al., 2014; Garel et al., 2007). These trends have been demonstrated using both in situ measurements of individuals and studies of museum collections. Image-based repositories have not yet been used for such purposes, despite their potential to increase understanding of the impacts of hunting pressure on animals. This is particularly the case for rhinos, owing to the high frequency with which they have been photographed over time.

In this study, we used the Rhino Resource Center (RRC), an online repository of rhino images and publications, as a data source to test the utility of online image repositories for large vertebrate research, and potentially research on other smaller but commonly

photographed taxa. Images on the RRC are uploaded by experts and obtained through extensive archival research and correspondence with authors and institutions. These images fall into two broad media categories—artwork and photographs. Collectively, artwork and photographs can provide important complementary information on how society viewed and interacted with rhinos, at the time the artwork or photograph was created. Photographs provide an extra benefit of showing 'true' representations of rhinos and therefore can be used to assess morphological changes over space and time. We focused on two key themes: (i) how the representation of rhinos in human culture has changed over time; and (ii) to what extent data on rhino morphology can be quantified from image repositories, with emphasis on horn sizes, and whether this has changed over time.

2 | MATERIALS AND METHODS

2.1 | Sample selection

All images used were taken from the RRC website: http://www.rhinoresourcecenter.com/. The RRC was founded in 2003 (Rookmaaker, 2003) and, at the time of this project, included a compilation of 23,123 files containing literature relating to all rhino species, and 4441 images within the Rhino Image Gallery (Rookmaaker, 2019). Images in this gallery are given species designations and an associated date and location where possible. We examined all images available in the RRC as of the 19th of March 2019. For each image, we extracted its associated date (either known based on the context of the image or estimated by the editors), identified the rhino species depicted (using the literature collection in the RRC to support our assertions where ambiguous), and classed it as either artwork or a photograph. We defined artwork as any image produced without the use of a camera, and photographs as an image of a rhino produced using a camera. A histogram of the relative representation of artwork and photographs in the RRC is available in Supplementary Material 2. We discarded images where no date could be inferred, where no species identification was possible, or where there was obvious repetition (1283 images). To more closely focus on the relationship between rhinos and society, we assigned all images into broad categories, representative of different relationships between rhinos and society. For artwork, these were 'Hunting', 'Conservation', 'Natural History', 'Captivity' or 'Other' and for photographs these were 'Hunting', 'Conservation', 'Natural History' and 'Captivity' (Table 1, Supplementary Material 1). We also used narrower categorisations to examine these trends on a finer scale, assigning artwork into one of 21 different narrow categories and all photographs into one of six narrow categories. Results using narrow categories without further grouping are available in Supplementary Material 3. In addition, narrow categorisations were further grouped into 'Consumptive' and 'Non-Consumptive' portrayals of rhinos, where consumptive use was defined as involving the death of rhinos

TABLE 1 Depiction categorisations and definitions for images available in the Rhino Resource Center (RRC). Categories were assigned by visual inspection of each image. Frequency of image types used for analyses of temporal trends given in brackets. Definitions for the narrow categories are available in Supplementary Material 1

Media type	Categorisation	Included narrow categories	Definition
Artwork (1531)	Hunting (137)	Hunting (137)	Non-photographed image featuring a human with a weapon aimed at a rhino, or a rhino that has been killed
	Conservation (71)	Conservation (49), caretaking (8), coexistence (8), peace (6)	Non-photographed image made to publicise the plight of rhinos or that depicts conservation management
	Captivity (62)	Captivity (62)	Non-photographed image showing a rhino in a zoo
	Natural history (995)	Nature (135), academic (117), curiosity (540), education (198), museum (5)	Non-photographed image made to showcase rhinos as a part of the natural world, without an explicit conservation focus
	Other (266)	Advert (25), cartoon (70), charge (94), dominion (24), fetishism (3), morphology (3), tourism (1), urbanisation (1), welfare (1), unknown (44)	Any non-photographed image which cannot be categorised as depicting either hunting or conservation
Photograph (1627)	Hunting (203)	Hunting (179), poaching (24)	Photograph where the rhino is either being hunted by humans or has been killed for a trophy or for its horn
	Conservation (182)	Conservation (182)	Photograph used to promote conservation efforts or which depicts conservation management
	Captivity (892)	Captivity (879), circus (13)	Photograph showing a rhino housed in either a zoo or a circus
	Natural history (350)	Nature (350)	Photograph produced to showcase rhinos as a part of the natural world, without an explicit conservation focus

or removal from their natural habitat (hunting, curiosity, museum, captivity, dominion, poaching and circus), while non-consumptive use did not kill or remove rhinos (all other narrow categories) (Duffus & Dearden, 1990) (Supplementary Material 1). Following consultation between two authors to establish categories, all categorisation was performed by a single author to reduce interauthor differences in characterisation and ensure consistency. Where an image fell into multiple categories, we prioritised 'Hunting' or 'Conservation', given their relevance to our study focus.

2.2 | Artwork

The RRC contains a range of artwork, with many themes (Table 1). In some cases, superficially similar artwork had alternative dates associated with it. In these cases, both pieces of artwork were included in the analysis given that this frequency was estimated at under 0.5% of total pieces of artwork and that superficially similar artwork might be used within different publications, and therefore represent truly different occurrences.

2.3 | Photographs

Repeated representation of a single individual reflects engagement with that individual. Therefore, all photographs were included in our analysis of changing relationships with rhinos over time, regardless of whether they depicted an individual that was also featured in another photograph (estimated at 33% of all photos). However, when analysing changing morphology over time, repeated photos of a single individual were excluded, to avoid any individual rhino having a disproportionate effect on analyses. We also identified whether photographs were taken of animals in the wild, in captivity (within a zoo or safari park) or in a sanctuary (close to natural conditions but with significant interference from conservationists, such as in the Sumatran Rhino Sanctuary at Way Kambas National Park, Indonesia), based on information given alongside the photographs.

2.4 | Morphometric measurements

To assess whether differences in rhino morphology could be identified between species, and whether rhino horn length changed over time, we measured several features of morphology on photographs of adult rhinos. We only included photographs where the animal was side-on to the camera to facilitate more accurate and repeatable measurements. We excluded photos of any individuals where the horn had been cut, as horn length varies substantially between rhino species and therefore is an important species-specific morphological trait. In total, we identified 80 images that were appropriate to use (22 black, 22 white, 18 Indian, 13 Sumatran and 5 Javan rhino images). We also recorded the captivity status of these rhinos. Of the 80 images, 3 were rhinos in a sanctuary, 12 were wild rhinos and 65 were captive rhinos.
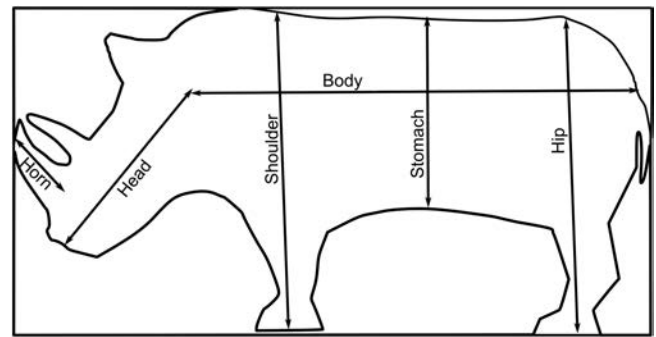

FIGURE 1 Morphometric measurements taken for each rhino in profile view on Fiji for ImageJ. Measurements are relative, given the absence of a scale bar. Silhouette by Hal Wilson.

All measurements were conducted using Fiji for ImageJ (Schindelin et al., 2012). Horn, body and head length, as well as stomach, shoulder and hip height were measured (Figure 1), using the location of skin folds as anatomical markers for these measurements. Head length was defined as the length from the end of the snout to the first skin fold of the neck. Body length was defined as the length from the last skin fold of the neck to the most posterior point on the body. Shoulder and hip height were the vertical length from the base of the foot to the dorsal surface in profile, and stomach height was the vertical distance from the most ventral point of the abdomen upwards to the dorsal surface. Horn length was defined as the distance from the tip to the base of the horn parallel to the long axis of the horn. Given the absence of a scale bar, all measurements were in arbitrary units.

2.5 | Data analysis

We performed all analyses in R Version 4.1.1. (R Core Team, 2020) and generated figures using *ggplot2* (Wickham, 2016).

2.6 | Changing perceptions of rhinos over time

When comparing the frequency of the different rhino species, we assigned different time bins for art and photographs, based on availability in the two media. For art, the time bins used were 'Pre 1850', '1850–1899', '1900–1949' and '1950 onwards', while for photographs, the bins were 'Pre 1920', '1920–1959', '1960–1999' and '2000 onwards'. Time bins for photographs were narrower due to no photographs being available prior to 1862 (and low numbers until the 20th century) and greater accuracy in date of production.

We used Chi-square tests or, when a cell in the contingency table had a value of 0, Fisher's Exact Tests to determine whether the frequency of representation of different species, broad categories ('Conservation', 'Hunting', 'Natural History', 'Captivity' or 'Other'), or 'Consumptive' and 'Non-Consumptive' uses changed over time. All tests were carried out separately for art and photographs and were based on the same time-bins as above. Poaching

was difficult to place for photographs because many images of poached animals were used for conservation publicity. We therefore retained this as a separate category and qualitatively assessed the effect of including it within either 'Hunting' or 'Conservation'. As it had negligible impact on the results, we included poaching images within 'Hunting' and present findings from this grouping in this paper.

2.7 | Morphological analyses

We used Bayesian generalised linear latent variable models (GLLVMs) (package BORAL; Hui & Blanchard, 2021) to test whether it was possible to detect differences between rhino species using our six relative measurements. This is a model-based analogue to traditional, distance-based methods that are used to analyse multivariate data, such as permutational analysis of variance (PERMANOVA). We fitted a pure (i.e. no covariates included) GLLVM (function boral; Hui & Blanchard, 2021) with two latent variables (LVs) and included a fixed row effect, since measurements were relative and to account for slight differences in angle and magnification between individual photographs. We fitted our GLLVMs to gamma distributions, since morphological measurements were non-negative continuous data. We ran models for 50,000 iterations using one chain and a thinning rate of 10, discarding the first 8000 iterations as burn-in. We fitted normal priors with mean zero and variance of 10 on all column-specific intercepts and LV coefficients. We fitted a half-Cauchy prior with mean zero and variance 5 on dispersion parameters and variance parameters in our models. We assessed mixing by visually inspecting MCMC trace plots. We validated our GLLVM by plotting Dunn-Smyth residuals against linear predictors, row indices, and column indices and ensuring no patterns were present. We also visually inspected Q-Q plots to ensure that a normal distribution was present (Hui, 2016). We visualised our analysis by plotting a two-dimensional ordination from the posterior medians of the LVs. We drew polygons around points from the same rhino species to aid visualisation. Polygons with more overlap indicated rhino species that were morphologically more similar. We compared positioning of polygons to the expected morphological differences between species based on phylogenetic position (Upham et al., 2019).

We used linear mixed effects models to investigate changes in relative horn length through time across rhino species (package LMERTEST; Kuznetsova et al., 2020). We performed regression analyses for horn length against every other relative measurement, and calculated R^2 values in each case with the MuMIn package (Bartoń, 2015). The highest R^2 value ($R^2 = 0.182$) was found using body length. We therefore calculated residual values for this regression, as a measure of horn length relative to body length for each individual. We then constructed a linear mixed effects model with the residual values as the response variable, year as a linear fixed effect and species as a random effect (function lmer) (Horn ~ Year + [Year|Species]). We tested a priori whether random

slopes were appropriate and validated this model by extracting residuals, plotting them against both Species and Year, and visually inspected the resulting plots following the methods of Zuur and Ieno (2016). The lmer function calculates t-tests using Satterthwaite approximations to degrees of freedom, which are robust to unequal variances and group sizes (Satterthwaite, 1946). We assessed whether Year was significant to the model and calculated the percentage of variance explained by fixed effects (marginal R^2, 'R^2_m') compared to a combination of fixed and random effects (conditional R^2, 'R^2_c') (Bartoń, 2015).

The high proportion of captive rhinos limited our ability to statistically test the impact of captivity on horn length. However, until the end of 1994, 68% of black rhinos, 57% of white rhinos and 65% of Indian rhinos in captivity were imported from the wild (Rookmaaker, 1998a, 1998b, 1998e), so that until the end of the 20th century, the majority of captive rhinos were either wild-born or first-generation captive-born, so we consider it likely they were still subject to selective pressures from processes affecting wild populations. The temporal distribution of captive and wild rhinos within this dataset was relatively uniform, so that it was not the case that recent years had a greater proportion of captive rhinos (Supplementary Material 4). We therefore consider it appropriate to use this dataset to investigate changing body proportions over time.

3 | RESULTS

In total, we identified 1273 images of Indian rhinos, 851 images of black rhinos, 603 images of white rhinos, 308 of Sumatran rhinos and 123 of Javan rhinos in the RRC dataset. The relative frequency of different rhino species in artwork changed significantly over time (Chi-square test, $n = 1531$, $\chi^2 = 481.61$, $p < 0.001$; Figure 2a). Early artwork had a higher representation of Indian rhinos, but the number of images of other species increased over time, particularly white rhinos since the mid-19th century. The relative frequency of different species in photographs also changed significantly over time (Chi-Square Test, $n = 1627$, $\chi^2 = 336.31$, $p < 0.0001$; Figure 2b), with a marked increase in the frequency of white, Sumatran, and Javan rhinos from the 1990s onwards.

3.1 | Changing depictions over time

There was a change in the relative frequency of depictions across categories in rhino artwork (Fisher's Exact Test, $n = 208$, $p < 0.0001$; Figure 3a) and photographs (Fisher's Exact Test, $n = 385$, $p < 0.0001$; Figure 3c) over time. In particular, depictions of hunting were more common in the early to mid-20th century, but depictions of conservation were more common in later images. Depictions of natural history and captivity also varied in frequency over time, with both becoming more common in photos from the 2000s onwards. The natural history category was particularly well represented in artwork prior to the start of the 20th century. Data from species differed in

their contribution to these patterns, with black rhinos being more commonly depicted in hunting images, Sumatran rhinos more commonly depicted in conservation images, and black, Indian and white rhinos being more commonly depicted in natural history and captivity images (Figure 3b,d).

We also found a similar shift in the frequency of representations of consumptive and non-consumptive use types in both artwork (Chi-squared test, $n = 1531$, $\chi^2 = 60.5405$, $p < 0.001$) (Figure 4a) and photographs (Chi-squared test, $n = 1627$, $\chi^2 = 66.1896$, $p < 0.001$) (Figure 4c), with a shift towards non-consumptive representations in artwork towards the end of the 18th century and in photographs from the 2000s onwards. Indian rhinos have consistently been illustrated in a consumptive context, while white rhinos are the rhino species most commonly photographed in a consumptive context today (Figure 4b,d).

3.2 | Morphological measurements

Morphology across rhino species differed, as indicated by the spatial separation of polygons in the ordination derived from our pure GLLVM, although there was considerable overlap (Figure 5). Black and white rhinos were more similar in morphology than Indian, Javan and Sumatran rhinos. Differences between species appeared most related to horn length and matched our expectation, based on phylogenetically related pairs of rhino species.

Relative horn length decreased significantly over time for all rhino species (Table 2, Figure 6). However, substantially more variation in horn length was attributed to species identity than time ($n = 80$, $t = -2.423$, $p = 0.0189$, $R^2_m = 0.028$, $R^2_c = 0.680$). While the rate of decline in horn length was found to be highest in Sumatran rhinos and lowest in white rhinos, the differences in slopes between the rhino species were negligible (Table 2, Figure 5).

4 | DISCUSSION

The RRC represents an extraordinary repository of information on rhinos stretching back more than 500 years for artwork and over 150 years for photographs. Over time, the representation of different species has changed, with Indian rhinos more commonly represented earlier in our dataset, and the two African rhino species more commonly represented in more recent images. There has also been a clear change in how rhinos are portrayed, with hunting scenes in both artwork and photos being more common pre-1950, but conservation being more common after this date. Depictions of natural history and captivity also became more common in artwork from the late 1700s onwards, and in photos from the 2000s onwards. The proportion of images featuring non-consumptive uses of rhinos also increased over time, although in this case from the turn of the 19th century. The number and quality of photographs represents a
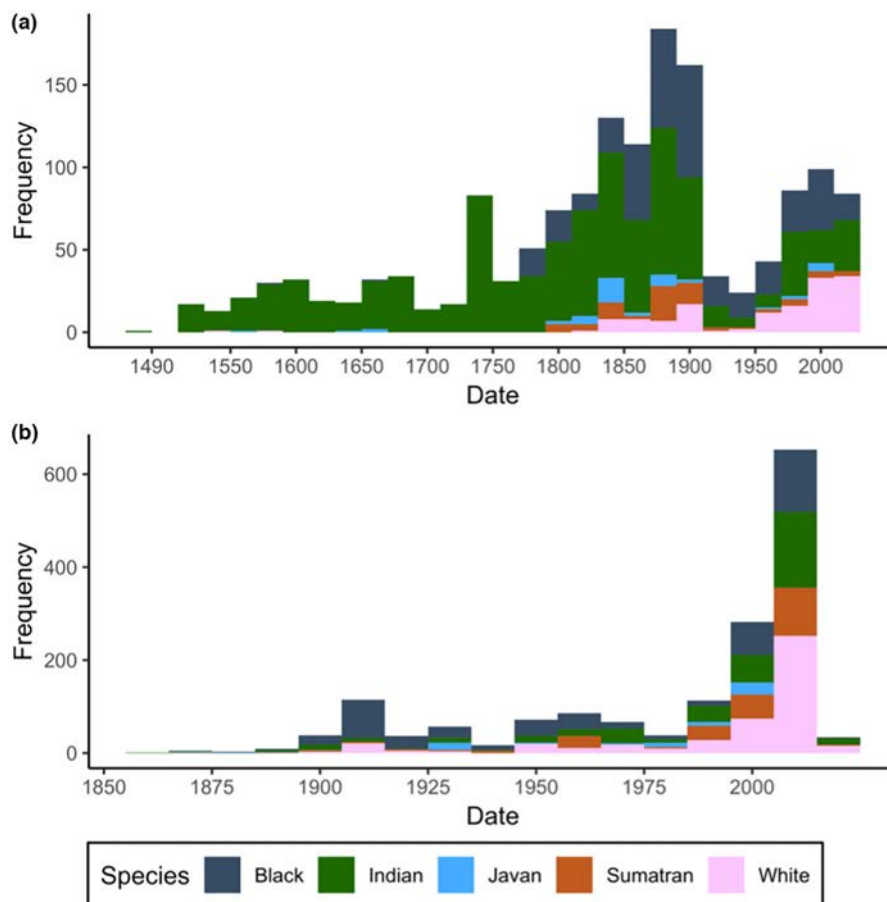

FIGURE 2 Changes in the representation of different rhino species in images in the Rhino Resource Center over time. (a) Species representation within artwork. (b) Species representation within photographs ($N_{black, photo} = 479$, $N_{Indian, photo} = 379$, $N_{Javan, photo} = 67$, $N_{Sumatran, photo} = 236$, $N_{white, photo} = 462$, $N_{black, art} = 374$, $N_{Indian, art} = 900$, $N_{Javan, art} = 45$, $N_{Sumatran, art} = 71$, $N_{white, art} = 141$).
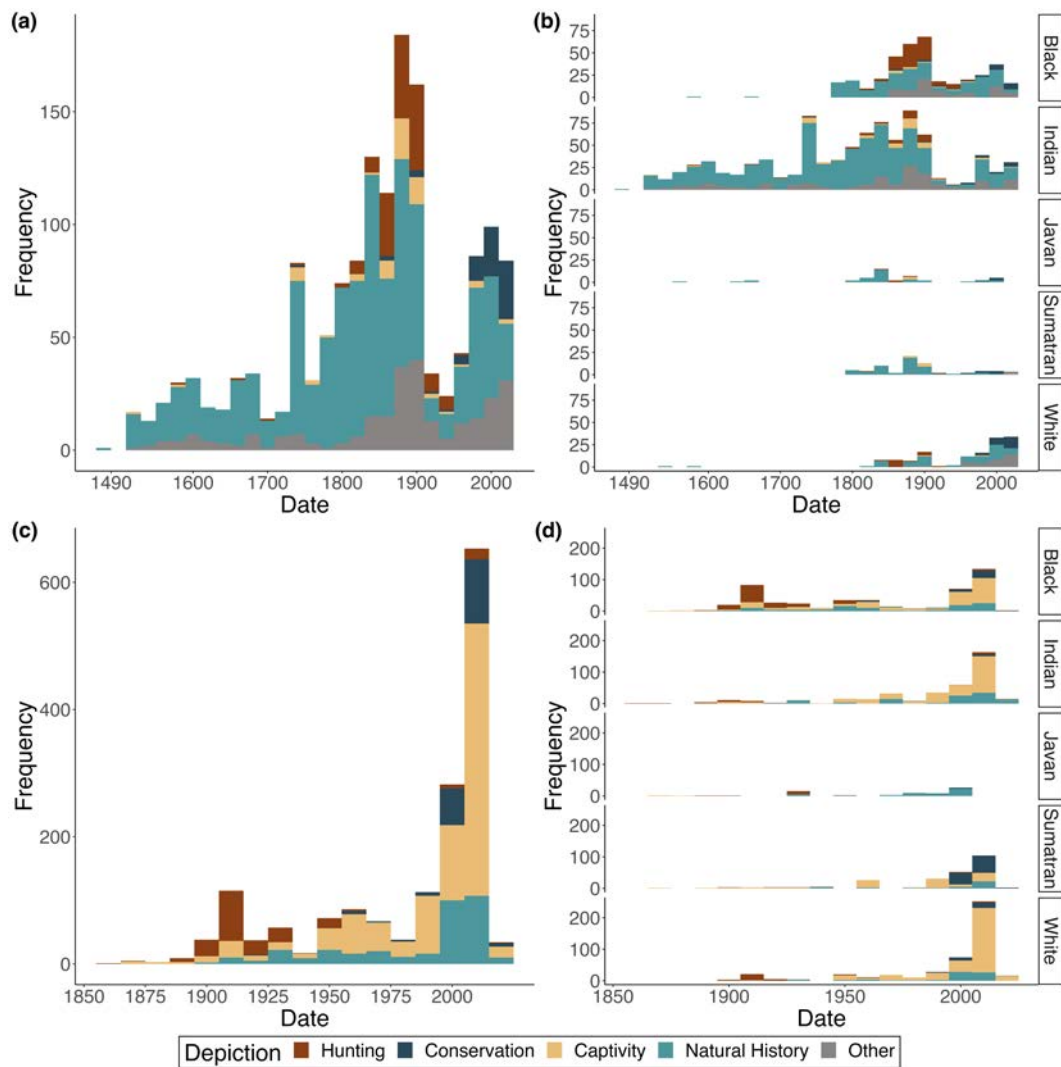
FIGURE 3 Changes in the depiction of rhinos in conservation, hunting, captivity, natural history and other categories from images on the Rhino Resource Center. (a) Relative depictions of different categories in artwork for all species, $N_{hunting, art} = 137$, $N_{conservation, art} = 49$, $N_{captivity, art} = 62$, $N_{naturalhistory, art} = 879$, $N_{other, art} = 266$, (b) relative depictions of different categories in artwork for each species individually, $N_{hunting, art, black} = 82$, $N_{conservation, art, black} = 22$, $N_{captivity, art, black} = 9$, $N_{naturalhistory, art, black} = 191$, $N_{other, art, black} = 70$, $N_{hunting, art, Indian} = 34$, $N_{conservation, art, Indian} = 14$, $N_{captivity, art, Indian} = 41$, $N_{naturalhistory, art, Indian} = 650$, $N_{other, art, Indian} = 161$, $N_{hunting, art, Javan} = 4$, $N_{conservation, art, Javan} = 4$, $N_{captivity, art, Javan} = 3$, $N_{naturalhistory, art, Javan} = 34$, $N_{other, art, Javan} = 0$, $N_{hunting, art, Sumatran} = 2$, $N_{conservation, art, Sumatran} = 7$, $N_{captivity, art, Sumatran} = 7$, $N_{naturalhistory, art, Sumatran} = 53$, $N_{other, art, Sumatran} = 2$, $N_{hunting, art, white} = 15$, $N_{conservation, art, white} = 24$, $N_{captivity, art, white} = 2$, $N_{naturalhistory, art, white} = 67$, $N_{other, art, white} = 33$ (c) relative depictions of different categories in photographs for all species, $N_{hunting, photo} = 203$, $N_{conservation, photo} = 182$, $N_{captivity, photo} = 892$, $N_{naturalhistory, photo} = 350$, (dD) relative depictions of different categories in photographs for each species individually, $N_{hunting, photo, black} = 122$, $N_{conservation, photo, black} = 42$, $N_{captivity, photo, black} = 215$, $N_{naturalhistory, photo, black} = 102$, $N_{hunting, photo, Indian} = 24$, $N_{conservation, photo, Indian} = 9$, $N_{captivity, photo, Indian} = 247$, $N_{naturalhistory, photo, Indian} = 99$, $N_{hunting, photo, Javan} = 13$, $N_{conservation, photo, Javan} = 5$, $N_{captivity, photo, Javan} = 3$, $N_{naturalhistory, photo, Javan} = 47$, $N_{hunting, photo, Sumatran} = 7$, $N_{conservation, photo, Sumatran} = 94$, $N_{captivity, photo, Sumatran} = 101$, $N_{naturalhistory, photo, Sumatran} = 35$, $N_{hunting, photo, white} = 37$, $N_{conservation, photo, white} = 32$, $N_{captivity, photo, white} = 326$, $N_{naturalhistory, photo, white} = 67$.

detailed dataset on rhino morphology, although the relatively similar proportions of different species indicated that our analyses primarily distinguished rhino species by horn length. Across all species, the horn length increased with body size, and the relative length of the horn to body length decreased over time. Taken together, our results demonstrate potential and scope for using online images to study the changing relationship between people and the natural world, and long-term morphological changes in species. We advocate a greater use of these data, and the development of more image repositories

such as the RRC, to bring data together in an easily accessible format with associated detailed information.

4.1 | Rhino representation in human culture

The RRC contains images of all five rhino species, though the relative commonness of these species in images is variable over time. The general overrepresentation of black and Indian rhinos
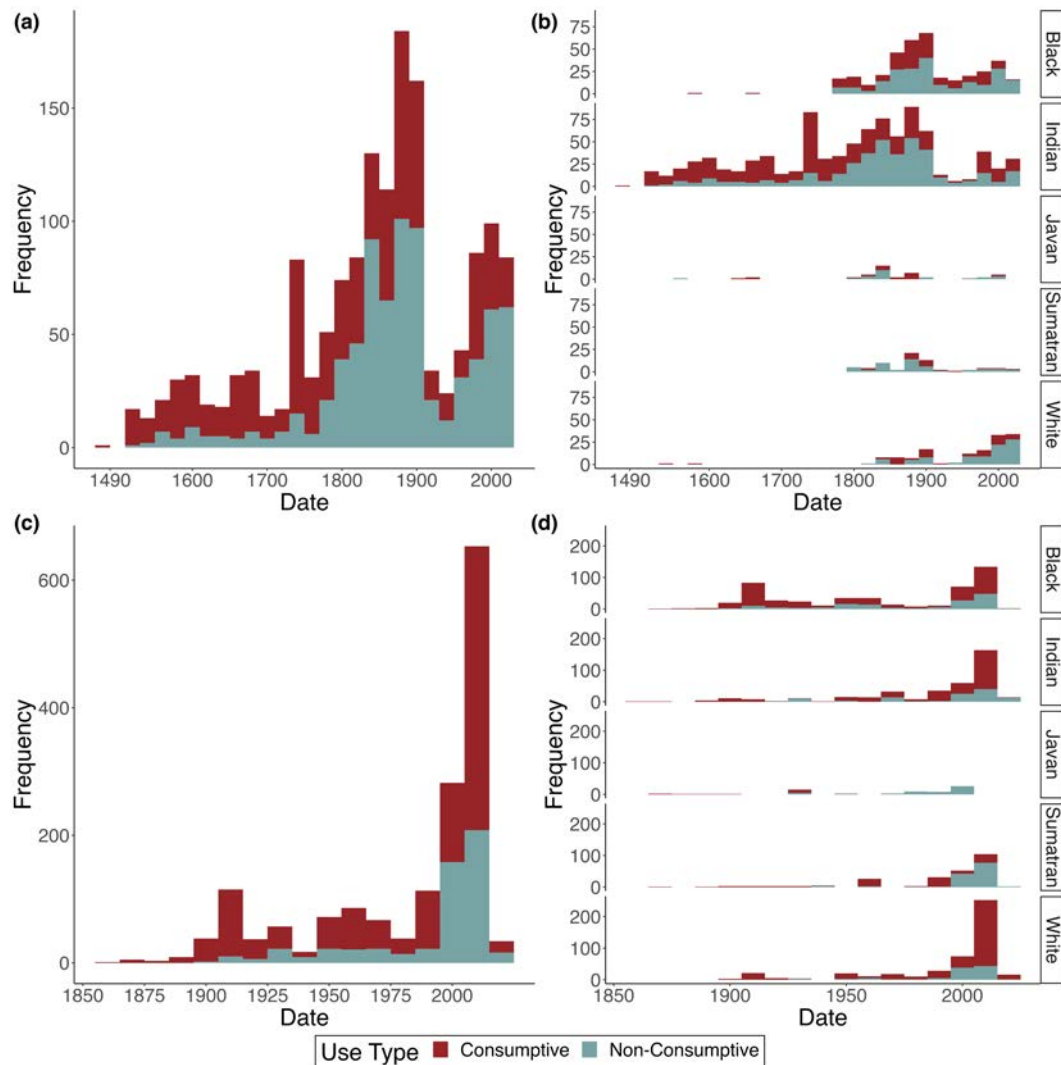
FIGURE 4 Relative frequency of consumptive and non-consumptive representations of rhinos in the Rhino Resource Center in (a) artwork for all species, $N_{consumptive,art} = 768$, $N_{non-consumptive,art} = 763$, (b) artwork for each species, $N_{non-consumptive,art, black} = 208$, $N_{consumptive,art, black} = 166$, $N_{non-consumptive,art, Indian} = 392$, $N_{consumptive,art, Indian} = 508$, $N_{non-consumptive,art, Javan} = 23$, $N_{consumptive,art, Javan} = 22$, $N_{non-consumptive,art, Sumatran} = 50$, $N_{consumptive,art, Sumatran} = 21$, $N_{non-consumptive,art, white} = 90$, $N_{consumptive,art, white} = 51$, (c) photographs for all species, $N_{consumptive,photos} = 1095$, $N_{non-consumptive,photos} = 532$ (d) photographs for each species. $N_{non-consumptive,photos black} = 144$, $N_{consumptive,photos black} = 337$, $N_{non-consumptive,photos, Indian} = 108$, $N_{consumptive,photos, Indian} = 271$, $N_{non-consumptive,photos, Javan} = 52$, $N_{consumptive,photos, Javan} = 16$, $N_{non-consumptive,photos,Sumatran} = 129$, $N_{consumptive,photos, Sumatran} = 108$, $N_{non-consumptive,photos, white} = 99$, $N_{consumptive,photos, white} = 363$.

within the RRC is likely a result of their more prominent position in European public consciousness due to greater accessibility for colonial explorers (Harris, 1838) and the presence of high-profile rhinos from these species in menageries of Europe during the Age of Discovery through the 15th to 17th Centuries (Rookmaaker, 1973). This is supported by the general increase in natural history and captivity representations of these two species in artwork from the end of the 18th century. However, since the middle of the 20th century, the frequency of white rhinos in the database has increased. The first captive white rhino was displayed at Pretoria Zoo in 1946 (Rookmaaker, 1998e), and the high number of recent photographs of this species is likely to be the result of high numbers currently in captivity (due to their relatively high captive longevity and birth rate). The numbers of photos of

all rhinos, but particularly black, Indian and white rhinos, have increased since the 2000s as captive rhinos are more easily photographed. In contrast, Javan and Sumatran rhinos have been kept in captivity far less often, with only 96 and 22 known specimens respectively by 1994 (Rookmaaker, 1998c, 1998d) and no specimens of either species in zoos or safari parks today. The more closed habitats occupied by these species have also precluded access by both hunters and tourists, and the inaccessibility of both wild and captive specimens explains the relative underrepresentation of these species in the RRC.

We found a clear shift in the focus of images over time, with images containing more hunting depictions pre-1950, but more conservation-focused depictions post-1950, as well as a similar shift from consumptive to non-consumptive use in artwork. This
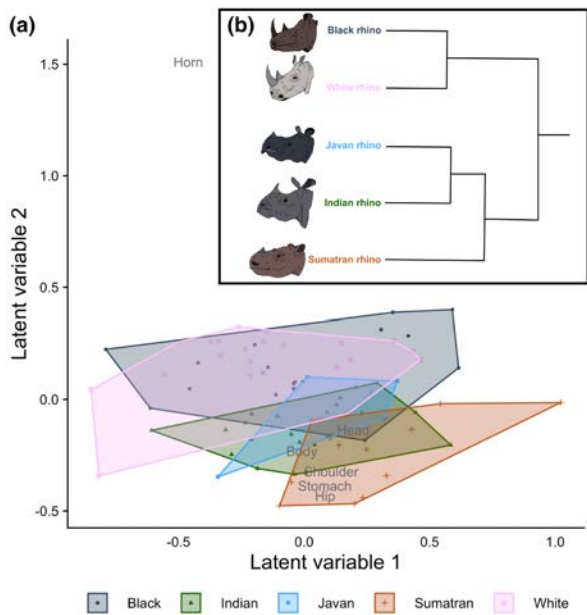
FIGURE 5 (a) Ordination generated from the pure generalised linear latent variable model (GLLVM). Points represent the posterior medians of the latent variables for each individual rhino photograph. Polygons have been drawn around points from the same species. Differences between species appeared most related to horn length, with black and white rhinos showing the longest horns and Sumatran rhinos the shortest horns. (b) Phylogenetic tree of modern rhinos, following Upham et al. (2019), illustrating that the position of polygons within the ordination matched the relative phylogenetic position of rhino species, with the black and white rhinos, and Indian and Javan rhinos respectively forming pairs both morphologically and phylogenetically.

TABLE 2 Predicted values from the mixed effects model for each rhino species. Mixed effects models were constructed using species as a random intercept effect, year as a fixed effect and random slope, and the residual values taken from a linear regression of horn length against body length as the response variable. Including rhino species as a random effect allowed for variable slopes for each species. Estimates for the slope are based on the estimate for the change in relative horn length of each species over time

Species	N	Intercept	Slope
Black	22	171.9393	−0.08305594
Indian	18	184.6263	−0.09878417
Javan	5	183.5632	−0.09746819
Sumatran	13	191.2171	−0.10696000
White	22	165.4831	−0.07505800

may reflect a change in the way rhinos are popularly viewed, and a growing awareness of the threats facing the natural world. The high number of photos showing consumptive use in the 21st century is again due to the presence and accessibility of rhinos in captivity rather than because more are being killed or removed from the wild. Though depiction categories had some level of subjectivity, we believe that the high sample size for these temporal analyses
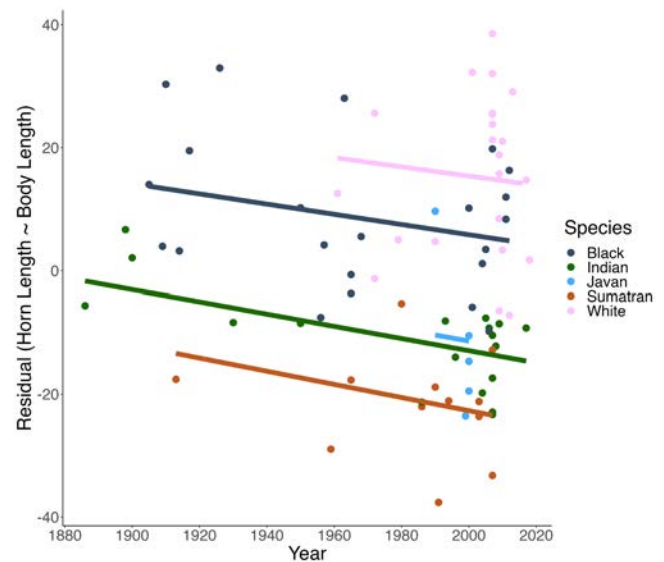

FIGURE 6 Scatterplot, showing changes in relative rhino horn length to body length over time for each rhino species, based on residuals from a mixed effects, random slopes linear model. Each point represents an individual rhino in a photograph on the Rhino Resource Center ($N_{black} = 22$, $N_{Indian} = 18$, $N_{Javan} = 5$, $N_{Sumatran} = 13$, $N_{white} = 22$). Y axis is the residual value taken from a linear model constructed for horn length against body length for the total dataset ($N = 80$). Slopes show the per-species change in the residual horn length over time from the mixed effects model (Table 2).

means that discrepancies in the placement of any individual image should have negligible effects on the overall results. It is likely that the number of hunting images for a given species is associated with the true hunting levels, given the high number of these images in the 19th and early 20th century. This in turn is likely to be correlated with reported declines in rhino numbers at this time, associated with hunting (Moodley et al., 2018). Therefore, we propose that online images of this kind could be used as a proxy for hunting pressure or other human interactions with wildlife. Such a use is likely to be particularly tractable for larger-bodied species as these are more likely to be photographed as a trophy, but could also be the case for other, smaller, but well-recorded taxa. The timing of increased hunting from our images was probably associated with a rise in the 'Empire mentality' at this time (MacKenzie, 1988), as peaks of hunting images appeared to be linked to the presence of European empires, and declines in hunting images occurred post-1950, during the collapse of European empires (Pearce, 2009).

The rise in the abundance of conservation imagery in the second half of the 20th century indicates that conservation awareness has increased over time, potentially benefitting conservation initiatives. Research on other threatened mammal species has demonstrated that stakeholder engagement in conservation is critical to conservation efforts (Howe et al., 2012; Ramesh & Jaunky, 2020; Vincenot et al., 2015). We suggest that a shift towards stakeholder engagement in rhino conservation will be similarly beneficial for all five rhino species. This shift is likely to be the result of increasingly

active conservation efforts in the field, through translocation and management, as well as public awareness campaigns. For example, one WildAid campaign in Vietnam reduced the number of people who believed that rhino horns have medicinal value by 67% in only 3 years (WildAid, 2017). Changes in attitude, legal changes related to rhino conservation, and active conservation in the field, are likely to have contributed to current population trends in rhinos, with populations of all species but the Sumatran rhino increasing (Emslie, 2006; Haryono et al., 2015; Lees, 2013; Yadava, 2014). In earlier time-periods, images were mainly produced by and for western societies and may have reflected pervading European views. However, as European empires collapsed and prevalence of rhinos in biological collections increased globally, the socioeconomic range of people both consuming and producing rhino images may have increased. As a result, images from later time-periods may reflect the attitudes and interests of a wider range of people.

The changing relationship between humans and rhinos that we detected in this study reflects larger-scale changes in how humans are interacting with and using the natural world. In particular, we detected a shift from consumptive uses of rhinos pre-1950s to generally non-consumptive uses after this period, although we note that there are a high number of images of captive rhinos in the 21st Century. The relationship between humans and nature is dynamic and variable across time and space (Mace, 2014), and there is growing consensus that nature's contribution to people can take the form of both relational and instrumental values (respectively reflecting more or less consumptive relationships) (Díaz et al., 2015; Kadykalo et al., 2019; Pascual et al., 2017). The provision of these contributions are determined not by nature itself but by human culture (Spangenberg et al., 2014). Given that images of rhinos reflect the lens through which these animals were viewed by society at the time they were created, our findings indicate that image repositories can represent a unique long-term dataset to study nature's contributions to people over time and human perceptions of nature. Here, we have distinguished between consumptive and non-consumptive images to reflect the change from generally material values placed on rhinos as status symbols and trophies, towards non-use values of rhino persistence (including the value of continued survival of wild species and bequest value), similarly observed in other mammal taxa (Macmillan & Phillip, 2008). The proportion of rhino images in the 'Natural History' category remained high throughout the period sampled (Figure 3), reflecting other non-consumptive values of rhinos, such as academic study and public curiosity about these animals.

4.2 | Online repositories as a source of morphological information

We found that morphological data on rhinos were available for the full range of species, demonstrating the potential of online images in morphological studies. Despite the low sample size, we were able to identify measurable morphological differences between species,

largely driven by horn size, with black and white rhinos appearing more similar to each other than Indian and Javan rhinos, reflecting their closer evolutionary relationship (Glaubrecht & Neiber, 2017; Margaryan et al., 2020; Price & Bininda-Emonds, 2009; Willerslev et al., 2009). Despite this, there was considerable overlap in morphology, reflecting real similarity in body proportions across rhino species. We also found a small but significant decline in relative horn length over time across all species. These results could be indicative of directional selection in response to hunting pressures, as has been noted in obvious features such as horns and tusks in other taxa (Chiyo et al., 2015; Coltman et al., 2003; Festa-Bianchet et al., 2014). In these cases, preferential hunting selection for individuals with larger horns or tusks resulted in individuals with smaller features surviving and reproducing more, passing on these traits to future generations, and resulting in an evolutionary change. These results are the first suggestion of a decline in horn length in rhinos in response to hunting pressures that we are aware of, and merit further research attention.

If further work demonstrates declines in rhino horn length in response to hunting pressures, this may have significant impacts on future rhino ecology. Different rhino species show different horn functionality. In Javan rhinos for example, the horn is a diagnostic secondary sexual characteristic (Griffiths, 1993), though not involved in fighting. Whilst seemingly not involved in direct female choice in white rhinos (Kretzschmar et al., 2020), horns are used in territoriality displays in this species through horn wiping of the surroundings, and show significant sexual dimorphism (Berger & Cunningham, 1994; Mazza, 1993). Black rhinos use their horns in intraspecific fights for social dominance (Berger & Cunningham, 1998), to defend against predators (Berger & Cunningham, 1994) and to assist in grasping vegetation (Mazza, 1993). Given the diverse functions of rhino horns, it seems likely that declining lengths could have a detrimental effect in defence or reproduction, though these effects will differ between species. Decreasing horn size may also increase the pressure on rhino populations through poaching, as more rhinos will need to be killed to meet demand for horn, which remains high (Cheung et al., 2021).

It is important to note that the captivity status of individuals in the measured photographs could have influenced our morphological findings. Indeed, the skulls of Asian rhinos have been found to differ in shape between wild and captive rhinos, suggesting captive rhinos are more challenging to use in morphological studies (Groves, 1982). Captivity has been found to significantly impact the strength of selection in other taxa (Allendorf & Hard, 2009; Mcphee & Mcphee, 2012; Schenekar & Weiss, 2017), and we would expect captive rhino populations to have weakened selection pressures for increased horn length, given a reduced requirement for territorial display. It could also be that a change in diet in captive rhinos could influence relative horn size of individuals. Although we are not aware of any study that has directly measured this effect, the dietary concentration of biotin has been found to affect the growth rate of the keratinous hooves of equids (Buffa et al., 1992), and nutrition has been found to be a key factor

influencing antler mass in several deer species (Harmel et al., 1989; Michel et al., 2016; Muir & Sykes, 1988). Whilst compositionally different, we consider it likely that diet may affect horn mass in rhinos in a similar way. The low sample size of wild rhinos (12 pictures) and rhinos in sanctuaries (3 pictures), and uneven distribution across species (e.g. all 5 photos of Javan rhinos in profile were taken in the wild) precluded statistical testing of the effect of captivity on horn length in this study. However, while we acknowledge that the captivity status of these rhinos may impact our results, the high proportion of wild-born or first-generation captive-born rhinos until the end of the 20th century, and the fact that both Sumatran rhinos and Javan rhinos are challenging to maintain and breed in captivity (meaning that almost all photographs of these species are wild-born) (Rookmaaker, 1998c, 1998d), mean that our conclusions on relative horn length are likely to be valid.

As photographs were not taken with the aim of assessing morphological changes through time, they typically did not contain any information about scale. As such, relative measures were required in this study. Using only profile-view photographs containing all six measurement features significantly reduced our sample size, with only 22 black, 18 Indian, 5 Javan, 13 Sumatran and 22 white rhino images. However, these 80 photographs demonstrate clearly the applicability of online image repositories for extracting morphological information, and future studies may choose less strict criteria in selecting images, such as including images with the head visible in profile, as has been done for artistic representations of the dodo (van der Geer et al., 2022). The rise of online repositories of information including images, such as iNaturalist (Mesaglio & Callaghan, 2021; Unger et al., 2021), also increases the scope of using images to study more recent morphological changes, using similar approaches to this study.

Natural history collections are biased towards certain parts of the world as a colonial legacy and therefore are inaccessible to many researchers (Aldrich, 2009; Lang et al., 2019; Raja et al., 2021; Stroud & Feeley, 2017), increasing the potential use of such image-based analyses. Rhino horns are particularly inaccessible, as many museums in Europe have moved original horns to secure facilities offsite or destroyed them, due to security risks (Grove & Thomas, 2016). Consequently, we propose that in this particular case, image-based research (supplemented by museum studies) is especially appropriate.

4.3 | Recommendations and future directions

The RRC currently represents a uniquely comprehensive image repository, although other websites such as the Saiga Resource Centre (www.saigaresourcecentre.com) and Tapir World (www.facebook.com/tapirworld) have begun to compile similar collections of images for other species. Our results show that online image repositories can provide a valuable tool for conservation. We therefore call for additional repositories to be created and used for conservation-focused research and to facilitate this work, we propose the following recommendations:

1. Focus on taxa that are most suitable for analysis (e.g. with notable morphological characteristics or frequently imaged taxa)—online image repositories are most useful when images are abundant. We therefore suggest that repositories focus on large mammals and other popular taxa, which are highly photographed (especially relative to other animal groups), easily recognisable in images, and more likely to be featured in artwork due to their popularity, while having a lower number of individual specimens in museum collections. Further, as many large mammals possess trophies (e.g. antlers, horns or tusks), photographs of these animals can facilitate analyses of morphological changes in response to changes in human behaviour or environmental conditions. Many medium-sized and small mammals should also be considered for image repositories, given that they can generally be identified to a species level from photographs (Kays et al., 2022), though they are unlikely to be as prominently featured in artistic representations. Groups such as voles, shrews and mice, which are difficult to differentiate between in photographs, are likely to be least suitable.

2. Include associated information with each image—for effective analysis, we suggest all images should have associated information recorded, including their location, date of production, species identification and original context. An associated literature bank alongside the images allows for further contextual information about the purpose of image production. Where possible, we recommend inclusion of a scale bar, for use in morphological analyses.

3. Engage with the general public to source images and publicise findings—engaging the general public with image databases (e.g. through social media) is likely to result in the inclusion of a greater variety of images from people with different backgrounds. With strict rules on associated metadata requirements, we believe that image repositories could be readily adapted into citizen science projects, with possible associated benefits for increased public understanding of science and conservation (e.g. Bonney et al., 2016; Callaghan et al., 2021). Indeed, community science-based repositories such as iNaturalist continue to grow, have a wide geographic range and contain images of captive animals in a similar way to the RRC. Existing data from these repositories could be combined with taxon-specific databases to increase engagement and maximise data availability (Mesaglio & Callaghan, 2021; Unger et al., 2021).

4. Engage with museums and other sources of biodiversity data to link image-based research with natural history collections—while there are challenges associated with using museum collections for large mammals, especially rhinos (e.g. an inability to collect new specimens, low number of individuals and security concerns), they continue to represent an invaluable resource. Where possible, we propose that image repositories should work alongside museums to include images and measurements of specimens within their collections, complementing ongoing efforts in the museum sector to fully digitise collections (Meineke et al., 2019). In addition, photo-vouchered specimens (such as produced by camera traps)

housed in databases like eMammal (Kays et al., 2020) represent a separate dataset with a known sampling effort that could be incorporated for a more complete view on the ecology of a given taxon.

5. Continue to build collections over time—once an image repository has been established, it must be maintained and consistently updated with both newly produced images and recently discovered images from historical records. This iterative collection requires dedicated editors and could, again, incorporate citizen science approaches in the gathering of images.

5 | CONCLUSIONS

Our results highlight the potential importance of online image repositories for addressing a wide range of biological research questions. They have the potential to provide a unique historical insight into how human-wildlife relationships have changed over time, as well as providing evidence for evolutionary change through captured morphological data. There is potential to expand this scope still further, for example by categorising habitat from images, demographic factors from images of groups of individuals, or past distributions of species from associated records. We acknowledge that there are methodological challenges to approaches using image repositories, such as biases and lack of scale bars on photographs. However, we have provided recommendations for how to use and enhance such data and believe that developing image repositories and databases to support such studies might be a particularly tractable approach for studying taxa with currently small populations or taxa from inaccessible areas, especially large vertebrate species that are commonly featured in art and photographs (e.g. elephants and tapirs). Given the rapid and accelerating loss of larger-bodied species worldwide (Malhi et al., 2016; Ripple et al., 2015), such work is particularly timely and may provide important information for informing species conservation approaches, as well as enhancing core biological knowledge.

CONFLICT OF INTEREST
We declare that both Edgar Turner and Kees Rookmaaker are members of the board of trustees for the Rhino Resource Center.

DATA AVAILABILITY STATEMENT
All data are available in the Apollo repository held by the University of Cambridge at https://doi.org/10.17863/CAM.88300

ORCID
Oscar E. Wilson https://orcid.org/0000-0002-4046-3128
Michael D. Pashkevich https://orcid.org/0000-0002-9033-8667
Kees Rookmaaker https://orcid.org/0000-0003-3121-5197
Edgar C. Turner https://orcid.org/0000-0003-2715-2234

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Digital image-based analysis from an online repository provides rich information on long-term changes in morphology and human perceptions of rhinos

Wilson OE[1,2], Pashkevich MD[2], Rookmaaker LC[3], Turner EC[2]

1. Department of Geosciences and Geography, University of Helsinki, Helsinki, Finland.
2. Department of Zoology, University of Cambridge, Cambridge, UK.
3. Rhino Resource Center, Utrecht, The Netherlands

Supplementary Material 1

Table S1. List and definitions of all narrow categorisations used for determining changing relationships between rhinos and society. 'Broad categorisation' describes which group each image was included in for the analysis shown in Figure 3. 'Use type' describes the groupings used for analyses shown in Figure 4

Media type	Narrow categorisation	Definition	Broad categorisation	Use type
Artwork	Hunting	Artwork featuring a human with a weapon aimed at a rhino, or a rhino that has been killed	Hunting	Consumptive
	Conservation	Artwork used to promote conservation efforts, or which depicts conservation management	Conservation	Non-consumptive
	Caretaking	Artwork showing humans providing rhinos with care e.g., at a wildlife sanctuary	Conservation	Non-consumptive
	Coexistence	Artwork showing humans and rhinos living side by side in harmony	Conservation	Non-consumptive
	Peace	Artwork showing rhinos in natural habitat with an obvious goal of portraying the rhinos in a generally positive light	Conservation	Non-consumptive
	Nature	Artwork showing rhinos in natural habitat without any other explicit focus	Natural History	Non-consumptive
	Academic	Artwork of a rhino used in a published piece of scientific research	Natural History	Non-consumptive
	Curiosity	Artwork of rhinos with the general aim of illustrating how unusual the animal is e.g., of rhinos in menageries shortly after discovery	Natural History	Consumptive
	Education	Artwork of rhinos included in books used to educate the public, especially children	Natural History	Non-consumptive
	Museum	Artwork of stuffed rhinos on display in a museum	Natural History	Consumptive
	Captivity	Artwork of rhinos in a zoo or safari park	Captivity	Consumptive
	Advert	Artwork using rhino imagery as part of an advertising campaign	Other	Non-consumptive
	Cartoon	Artwork in a cartoon style that shows a stylised rhino, still identifiable to species level	Other	Non-consumptive
	Charge	Artwork showing a rhino charging at humans or domestic animals with no gun featured. These images show rhinos as aggressive animals	Other	Non-consumptive
	Dominion	Artwork showing humans as being superior to rhinos in some way, without directly showing hunting e.g., using rhinos to pull trailers	Other	Consumptive
	Fetishism	Artwork showing rhinos in sexually suggestive positions, often involving their horn	Other	Non-consumptive
	Morphology	Artwork showing some specific feature of rhino morphology e.g., horn but not fitting into other categories	Other	Non-consumptive
	Tourism	Artwork illustrating rhinos as a tourist attraction	Other	Non-consumptive
	Urbanisation	Otherwise-neutral artwork showing rhinos in densely populated areas e.g., cities or towns	Other	Non-consumptive
	Welfare	Artwork drawing attention to animal welfare issues as pertaining to rhinos	Other	Non-consumptive
	Unknown	Artwork that doesn't fit into any other category	Other	Non-consumptive
Photograph	Hunting	Photo featuring a human with a weapon aimed at a rhino, or a rhino that has been killed as part of an organised trophy hunt	Hunting	Consumptive

	Poaching	Photo of a rhino with horn removed by poachers (not part of an organised trophy hunt)	Hunting	Consumptive
	Conservation	Photo used to promote conservation efforts or which depicts conservation management	Conservation	Non-consumptive
	Nature	Photo of rhinos in natural habitat with no other explicit focus	Natural History	Non-consumptive
	Captivity	Photo of rhinos in a zoo or safari park	Captivity	Consumptive
	Circus	Photo of rhinos performing in a circus show, or housed in a circus	Captivity	Consumptive

Supplementary Material 2
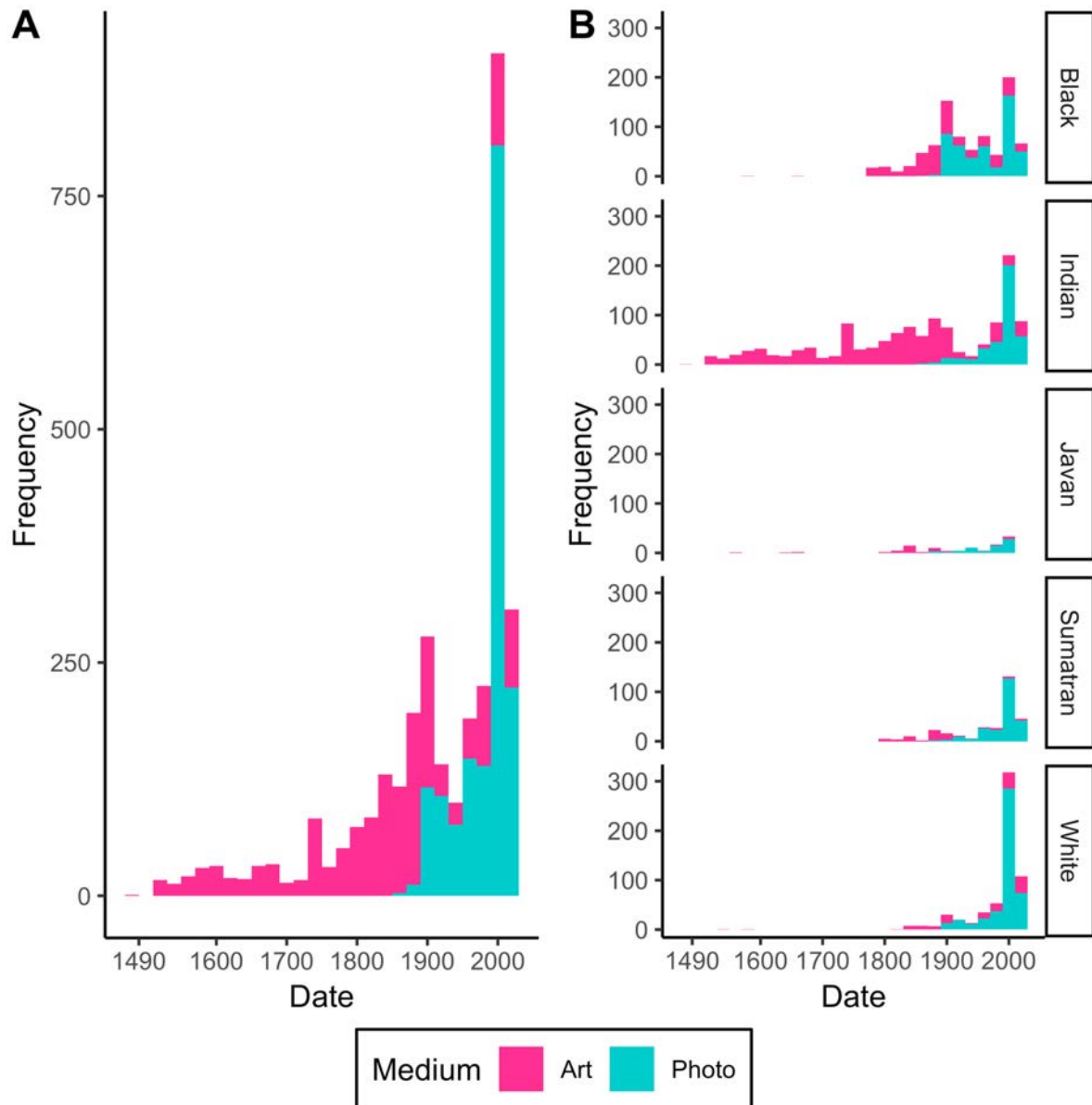
Figure S1. Change in media used to produce images on the Rhino Resource Center. A) The frequency of artwork and photographs for all species (N_{total} = 3,158, N_{photo} = 1,623, $N_{artwork}$ = 1,531). B) The frequency of artwork and photographs for each species individually ($N_{black, photo}$ = 479, $N_{Indian, photo}$ = 379, $N_{Javan, photo}$ = 67, $N_{Sumatran, photo}$ = 236, $N_{white, photo}$ = 462, $N_{black, art}$ = 374, $N_{Indian, art}$ = 900, $N_{Javan, art}$ = 45, $N_{Sumatran, art}$ = 71, $N_{white, art}$ = 141). Photos are defined as any image produced using a camera, and the first recorded photograph within the dataset is from 1862. Artwork includes all other images, and includes images dated from 1491 onwards.
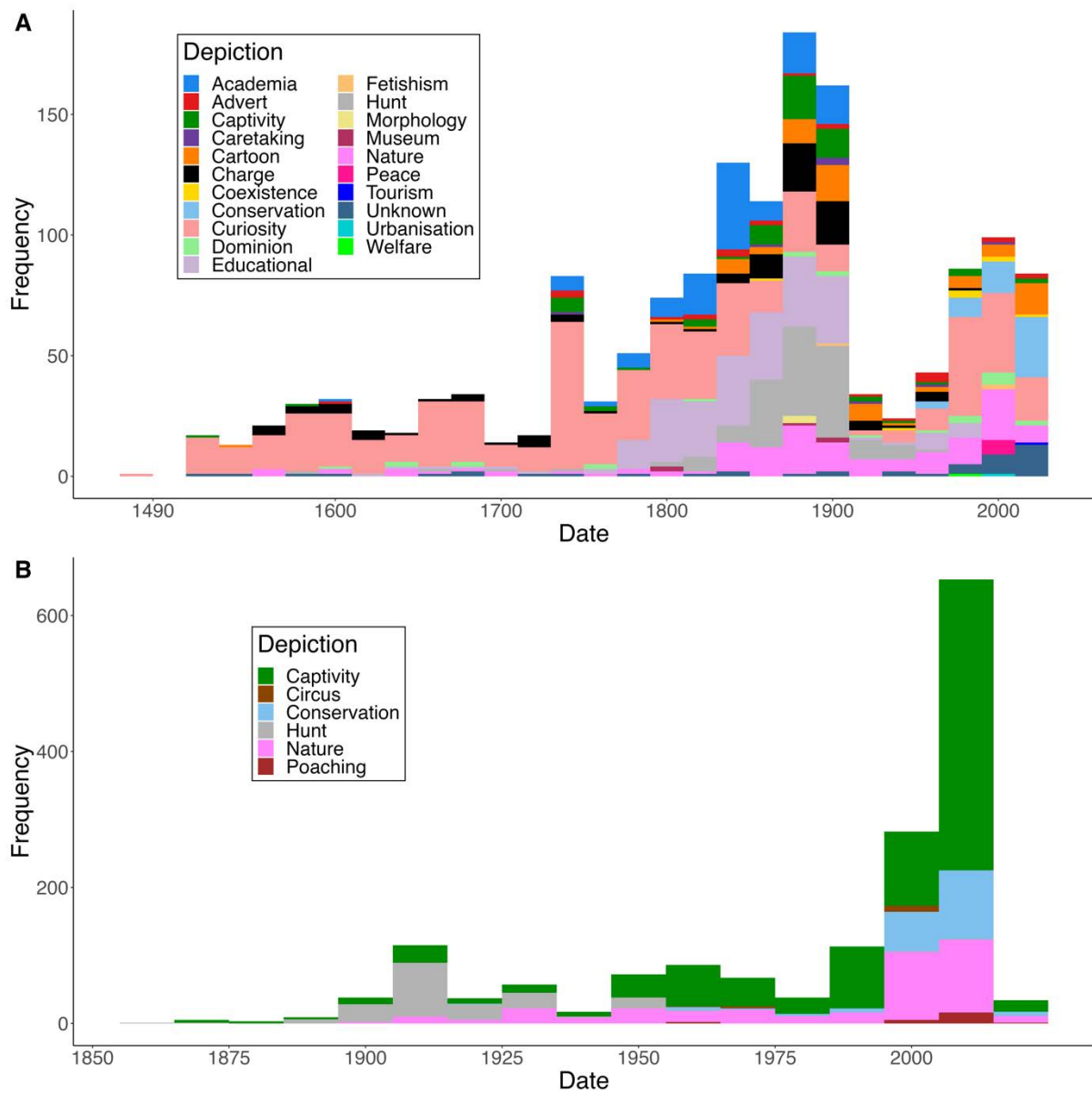
Supplementary Material 3

Figure S2. Changes in the depiction of rhinos over time from images on the RRC using the narrow categorisations rather than grouping into 'Hunting', 'Conservation', 'Natural History' and 'Other' as in Figure 3. (A) Rhinos in artwork, (B) Rhinos in photographs
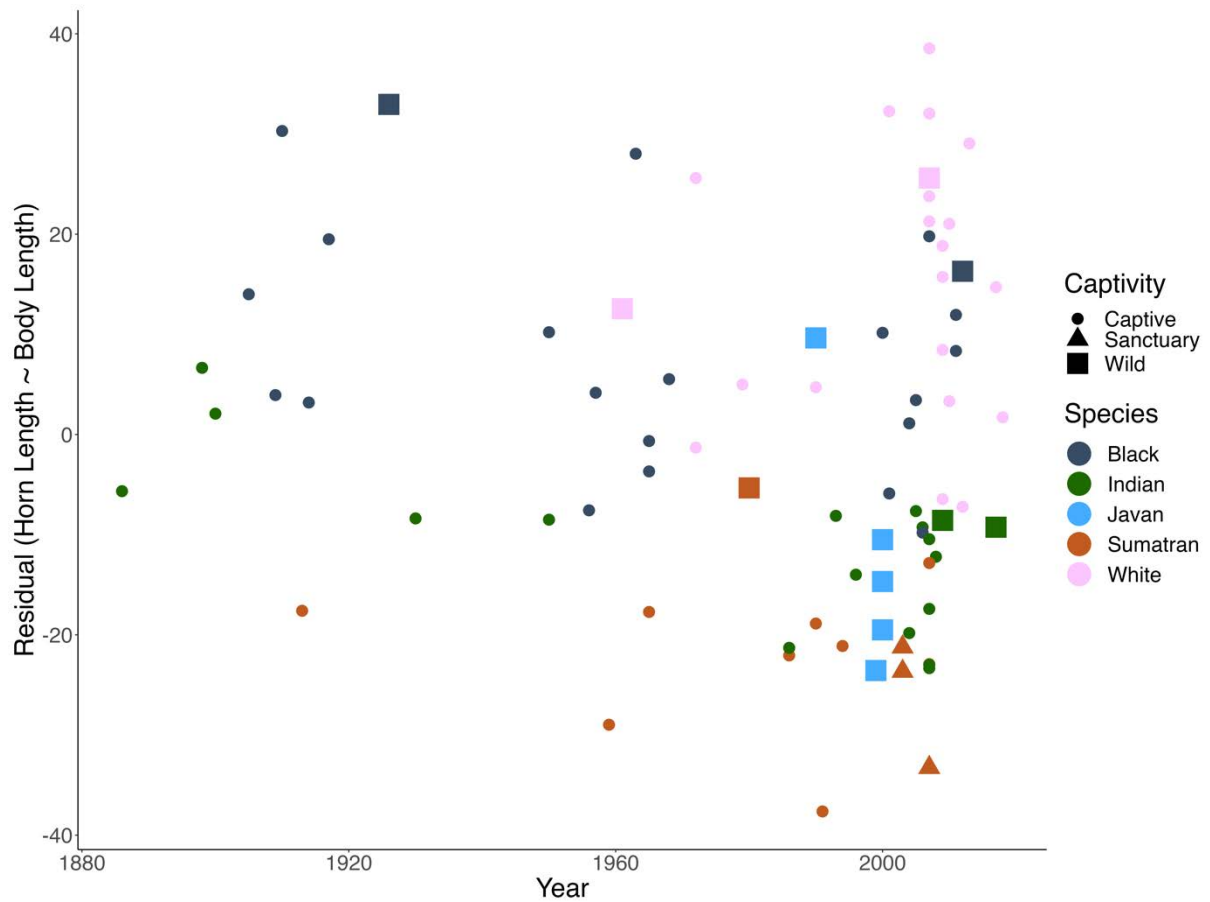
Supplementary Material 4

Figure S3. Distribution of the different captivity statuses in the rhino dataset used for modelling changing horn length over time. Each point represents a different photograph, with photograph year on the x axis and the residual value from the relationship between horn length and body length on the y axis. Different rhino species are represented with different colours and different captivity statuses with different shapes. To make them stand out given a lower number of points, the wild-photographed rhinos are highlighted as larger points.
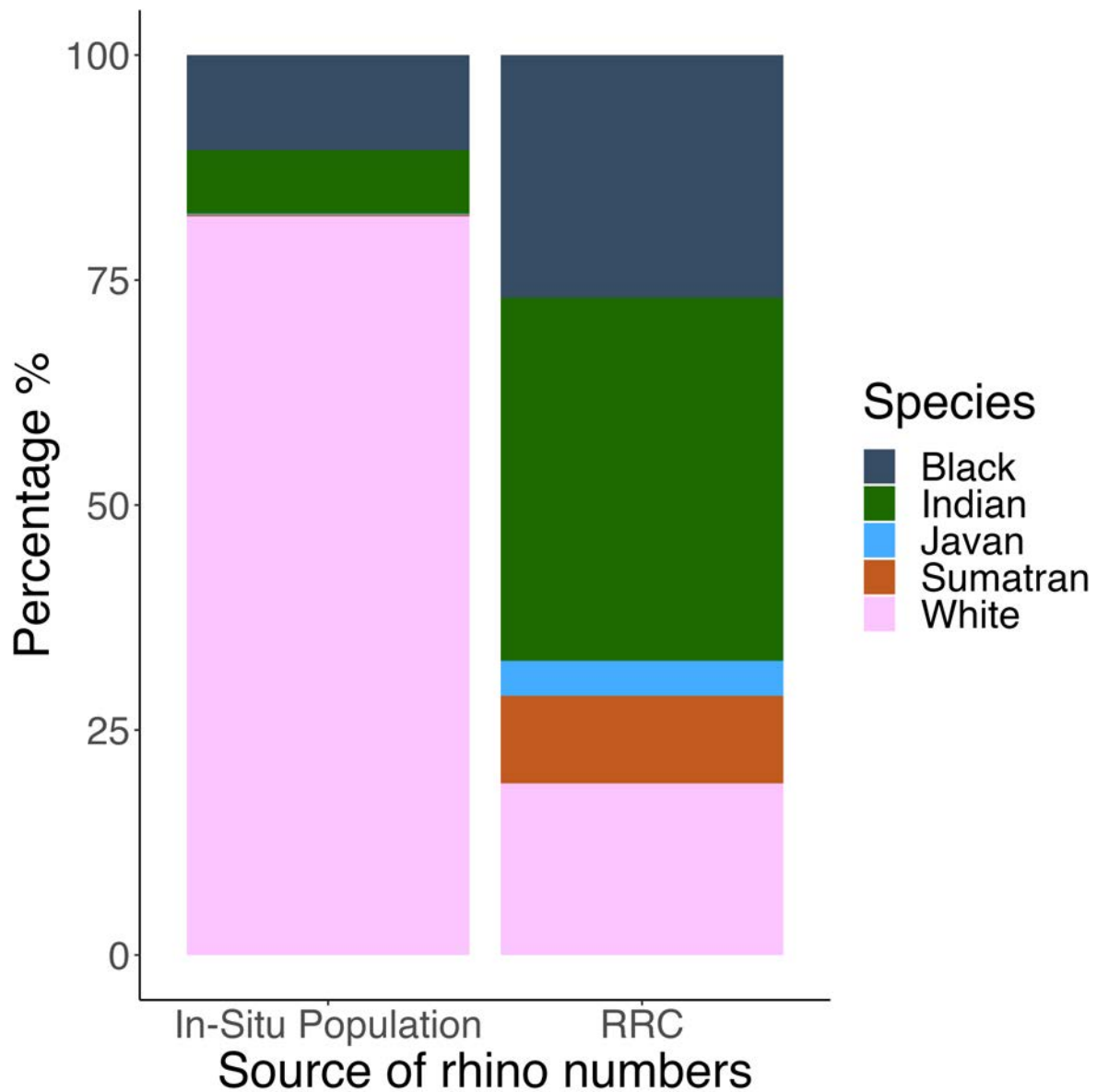
Supplementary Material 5

Figure S4. Number of images on the Rhino Resource Center compared to the estimated in situ population size of each species. Percentage is the number of actual or portrayed rhinos of a given species as a percentage of the total number of actual or portrayed rhinos (($N_{black, population}$ = 5249, $N_{Indian, population}$ = 3500, $N_{Javan, population}$ = 67, $N_{Sumatran, population}$ = 80, $N_{white, population}$ = 40,751, $N_{black, images}$ = 854, $N_{Indian, images}$ = 1277, $N_{Javan, images}$ = 123, $N_{Sumatran, images}$ = 308, $N_{white, images}$ = 603). In-situ population sizes were obtained from Save The Rhino (*https://www.savetherhino.org/rhino-info/population-figures/*, accessed April 2019). Where there was a population range, we took the mean of the upper and lower bounds as an estimated population size.